COMPARISON OF MORPHOLOGICAL AND MOLECULAR PHYLOGENY OF THE DECAPODA

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Decapod phylogenies based on morphological and molecular data are similar in topology for the taxa in common; both trees recognise a dendrobranchiate lineage, a caridean lineage (including procaridids), a stenopodidean lineage, and a reptant lineage. The two trees are compared with respect to homoplasy levels using consistency indices, homoplasy excess values, and bootstrap values for the various nodes. In all cases the molecular data exhibit considerably less homoplasy. It is suggested that molecular and morphological data be viewed as complementary because in many cases comparative morphology has suggested the research question. Significant questions on decapod phylogeny remain with the reptant infraorders. ☐ *Decapoda, phylogeny, morphology, molecular data, nucleotide sequences, 18S ribosomal RNA.*

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Decapods are among the best known of the crustaceans, although their phylogenetic relationships are poorly understood. Recent reviews of decapod phylogeny (Burkenroad, 1963, 1981; Glaessner, 1969; De Saint Laurent, 1979a; Felgenhauer and Abele, 1983; Abele and Felgenhauer, 1986) have resulted in recognition of a fundamental division of the decapods into two groups, the Dendrobranchiata (penaeid shrimp and their relatives) and the Pleocyemata (all other decapods). This division is based on the fact that all pleocyemates incubate their embryos on the pleopods, with eclosion occurring at a zoeal or later larval stage, in contrast to dendrobranchiates and euphausiaceans, which release embryos free into the sea with eclosion occurring at a naupliar stage. Furthermore, dendrobranchiates have a unique gill morphology consisting of a central branchial axis and paired lateral branches each with subdivided secondary rami (= the dendrobranchiate condition). The male petasma might also be a unique dendrobranchiate feature as Burkenroad (1963) suggested that this structure is not homologous to that found in euphausiaceans and some reptants. All other morphological characters generally cited for dendrobranchiates are either found in other taxa or are pleisiomorphic and uninformative relative to the Decapoda.

The above analyses and diagnoses were based on morphology, while the analysis of Kim and Abele (1990) used nucleotide sequences of 18S ribosomal RNA in a phylogenetic study of selected decapods. Here I briefly review the classification and phylogeny of the Decapoda and, using new sequence data for a dendrobranchiate, several carideans and a brachyuran crab, compare molecular results to those obtained from morphological data.

MATERIALS AND METHODS

A summary classification of the Decapoda is given in Table 1 along with a list of the decapod taxa used in this study. Kim and Abele (1990) provided details on sequencing methods and alignment of the sequences, and all molecular data have been deposited in GenBank. The list of morphological characters is given in Appendix I (derived from Abele and Felgenhauer, 1986, figs 2–5). Phylogenetic analyses were performed using PAUP 3.0 (Swofford, 1990). A dendrobranchiate shrimp, *Penaeus aztecus*, was used as the outgroup for the molecular data while *Euphausia* sp. was used as the outgroup for the morphological data.

RESULTS

MOLECULAR ANALYSIS

Maximum parsimony analysis yielded a single minimum-length tree (Fig. 1a) of 432 steps with a consistency index of 0.692 based on 195 phylogenetically informative characters. The two dendrobranchiates are joined by a node (A) that is 35 steps from the node (B) joining the pleocyemates (*Penaeus aztecus* is 17 steps from the node (A) while *Sicyonia brevirostris* is 40 steps from

TABLE 1. Summary classification of the Decapoda (modified from Bowman and Abele, 1982) with respect to the taxa used in this study.

	Number of Nucleotides
Decapoda	
Suborder Dendrobranchiata	
Family Penaeidae	
Penaeus aztecus Ives	1,301
Family Sicyoniidae	
Sicyonia brevirostris Stimpson	884
Suborder Pleocyemata	
Infraorder Caridea	
Family Alpheidae	
Alpheus heterochaelis Say	898
Family Atyidae	
Typhlatya rogersi Chace and Manning	995
Family Procarididae	
Procaris ascensionis Chace and Manning	869
Family Palaemonidae	
Palaemonetes kadiakensis Rathbun	1,153
Infraorder Stenopodidea	
Family Stenopodidae	
Stenopus hispidus (Olivier)	1,315
Infraorder Astacidea	
Family Astacidae	
(several taxa, morphological data)	
Family Cambaridae	
Procambaris leonensis Hobbs	1,721
Infraorder Thalassinidea	
Family Axiidae	
Coralaxius abelei Kensley and Gore (morphological data)	
Infraorder Brachyura	
Family Raninidae	
Ranilia muricata H. Milne Edwards	1,127
Family Portunidae	

the node). The next branch off the tree (B-C) is 33 steps and leads to a node (C) that joins all caridean shrimp, including *Procaris ascenscionis* which comes off this node (C) with a branch length of 19; a relatively long branch (C-D) of 52 steps leads to a node (D) joining the three remaining caridean shrimps [an atyid, *Typhlatya rogersi*, comes off first with a branch length of 27 steps followed by a branch (D-E) of 24 steps leading to a node (E) joining an alpheid, *Alpheus heterochaelis*, with a branch length of 19 steps and a palaemonid, *Palaemonetes kadiakensis*, with a branch length of 14 steps]. Returning to the main branch, there is a segment (B-F) of 28 steps with a side branch of 35 steps leading to a stenopidid shrimp, *Stenopus hispidus*. The next branch (F-G) is 38 steps and leads to a node (G) with one branch of 11 steps leading to the crayfish *Procambarus leonensis*; the next branch (G-H) is 14 steps and leads to a node (H) that joins two brachyuran crabs, *Ranilia muricata* with a branch length of 8 steps and the blue crab *Callinectes sapidus* with a branch length of 18 steps.

The data were also evaluated by the bootstrap method (Felsenstein, 1985) which involves random sampling of the original data set with replacement until a new data set equal in size to the original is obtained. Each of the new data sets (in this case 100) is analyzed using maximum parsimony and the number of times each node occurs is recorded. This method provides an indication of the level of support for each node in the tree with 95% considered to be statistically significant. The bootstrap value joining the two dendrobranchiates is 95% while that of (B) joining all pleocyemates is 94%. The values for the caridean shrimps (C, D, E) are 99–100%. The value for the node (F) joining the so-called reptant taxa is 86%, if *S. hispidus* is considered a member of this group. The value is 96% (node G) for taxa traditionally considered to be reptants and the value for the node joining the two brachyuran crabs is 100%. These results suggest considerable support for the relationships diagramed in Fig. 1a.

MORPHOLOGICAL ANALYSIS

Maximum parsimony analysis of the morphological data using *Euphausia* sp. as the outgroup yielded a single minimum length tree (Fig. 1b) of 74 steps with a consistency index of 0.568 based on a total of 40 phylogenetically informative characters. The first branch to come off the tree with a length of 3 steps leads to *Penaeus*; this is followed by a branch that leads to a node (C) joining *Procaris* (5 steps) and a caridean (8 steps); the next branch leads to *Stenopus* (2 steps) while the terminal node joins an axiid (9 steps) and an astacid crayfish (2 steps).

A bootstrap analysis reveals limited support (55%) for the pleocyemate lineage (node B) and somewhat larger values for the Caridea (67%, node C), the Stenopididea (65%, node D) and the Reptantia (82%, node E).

DISCUSSION

COMPARISON OF TREES

Comparison of Fig 1a and 1b reveals that the two trees have similar topologies for the taxa in common. Both trees recognize a dendrobranchiate lineage separate from all other decapods,

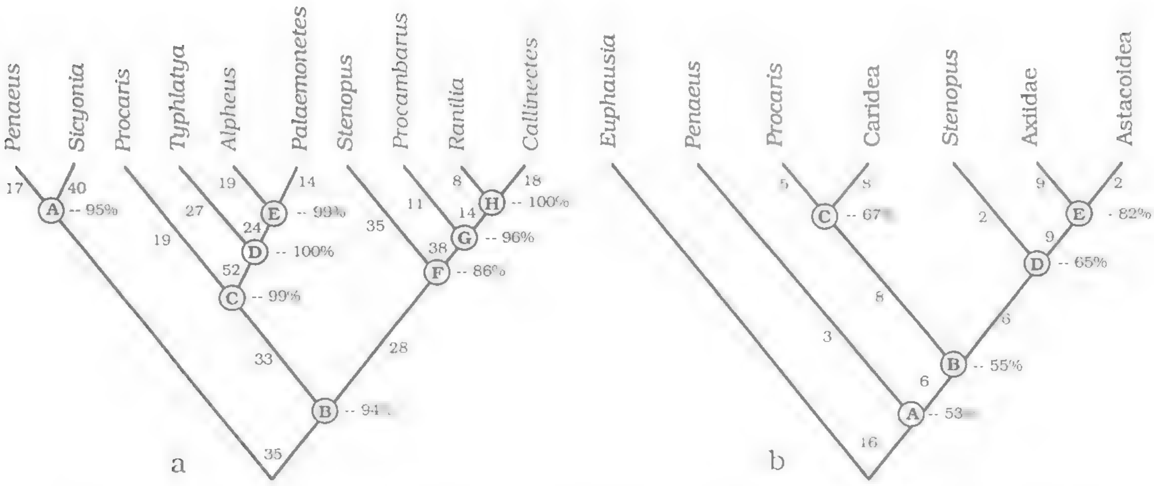

FIG. 1. Relationships among the taxa shown as inferred by maximum parsimony analysis. a, based on nucleotide sequences of 18S ribosomal RNA, tree length = 432 steps based on 195 characters, CI = 0.692. b, based on morphological data, tree length = 74 steps based on 40 characters, CI = 0.568. % numbers adjacent to nodes are bootstrap values based on 100 replicates.

a caridean lineage, a stenopodidean lineage and a reptant lineage.

There are several approaches to comparing and evaluating the reliability of phylogenetic hypotheses based on maximum parsimony (Archie, 1989b). A common approach has been to compare consistency indices (CI) among the trees. CI is the minimum number of steps on the tree when no homoplasy is present divided by the observed number of steps. While this seems a reasonable approach to use, Archie (1989a) showed that the CI is highly and negatively correlated with the number of taxa and proposed another statistic for comparative purposes. In the present case the number of taxa does not differ much (7 *vs* 10) and the CI for the molecular data set of 10 taxa is higher than that for the morphological data (0.692 *vs* 0.568). Another approach (Archie, 1989b) is to compare the maximum number of steps possible on a tree to both the minimum possible and the observed number of steps.

For the morphological data the maximum tree length is 104, the minimum length is 42 while the observed is 74. Archie (1989b) suggested using these values to calculate a ratio, HERM (= homoplasy excess ratio maximum), which is the maximum number of steps minus the observed divided by the maximum number minus the minimum possible number of steps. Thus the value is 1 when no homoplasy is present and 0 when there is no phylogenetic information in the data. For the morphological data, HERM = 0.484. This somewhat low value is not unexpected given the relatively low bootstrap values obtained for each of the tree nodes (Fig. 1b). An examination of the characters mapped out on the tree reveals that 25 of the 40 reverse at least once and only 15 (indicated by an asterisk in Appendix I) map without homoplasy. It is interesting to note that of the latter 15 characters, 10 are concerned with the presence/absence of exopods and gills on the pereiopods.

The molecular data demonstrate considerably less homoplasy. The maximum tree length (without *Sicyonia*, which was dropped to facilitate comparisons) is 508, the minimum possible is 275 and the observed is 340 resulting in a homoplasy excess ratio maximum (HERM) of 0.721. This relatively high value is consistent with the high bootstrap values obtained (Fig. 1a).

Does this mean that molecular data are more reliable than morphological data with reference to decapod phylogeny? Probably not as it may be possible to select a different suite of morphological features with less homoplasy. It should also be emphasized that a single morphological character may be of such fundamental biological importance that it alone can provide strong evidence for evolutionary relationships. No single nucleotide site could ever provide such evidence. The morphological and molecular data sets should be viewed as complementary. Centuries of comparative morphology have provided the background and in many cases posed the interesting questions that may be further investi-

TABLE 2. Comparison of data derived from parsimony analyses of morphological and molecular data.

	Molecular	Morphological
Number of Taxa	10	7
Number of Variable Characters	582	57
Number of Phylogenetically Informative Characters	195	40
Tree Length	432	74
Consistency Index	0.692	0.568
HERM	0.721	0.459
Bootstrap values		
Pleocyemata	94%	55%
Caridea	100%	67%
Stenopodidea	86%	65%
'Reptantia'	96%	82%
Brachyura	100%	NA

gated with molecular data. For example, the comparative morphological investigation of Wingstrand (1972) on pentastome spermatozoan morphology posed the question of their relationship to crustaceans that caused Abele *et al.* (1989) to further test (and support) this relationship using molecular data. What that study and the present one do indicate is that nucleotide sequences of 18S ribosomal RNA are reliable data for reconstructing crustacean phylogenies.

STATUS OF DECAPOD PHYLOGENY

Analyses of morphological data (Burkenroad, 1963, 1981; Schram, 1984; Abele and Felgenhauer, 1986) suggested abundant support for the recognition of the Dendrobranchiata. Kim and Abele (1990) provided molecular evidence in support of this group and inclusion here of a second dendrobranchiate (*S. brevirostris*) supports these previous results. Although Abele and Felgenhauer (1986) discussed reasons for rejecting the concept of a taxon Natantia (originally defined to include penaeids, stenopodids and carideans), the term is occasionally used in defining spermatozoan types because penaeids, procaridids and carideans all have 'unistellate' or thumbtack spermatozoa (Jamieson, 1991; Felgenhauer and Abele, 1991). In contrast, stenopodids, the other so-called natant, have a very different spermatozoan structure (Felgenhauer and Abele, 1991) and I would only repeat an earlier conclusion (Burkenroad, 1963; Abele and Felgenhauer, 1986) that there is little evidence to support the concept of a Natantia and many reasons for rejecting it.

Additional questions on classification and relationships centre on taxa in the suborder Pleocyemata. One area of discussion concerns the limits of the Caridea and whether or not it includes procaridid shrimp. Schram (1986) recognized two infraorders, the Procarididea and Caridea, placing them in the Suborder Eukyphida, a term coined by Boas for carideans and resurrected by Burkenroad (1981) and Schram (1984, 1986). The disagreement is really one of terminology because there is ample morphological evidence that procaridids and carideans share a common origin (Abele and Felgenhauer, 1986; Kensley and Williams, 1986; Schram, 1986), a conclusion that is strongly supported by the molecular data presented here. It is also clear that procaridids are separated from other carideans by a relatively long molecular distance (52 steps, Fig. 1a) as well as by differences in gill formulae (Burkenroad, 1984; Abele and Felgenhauer; 1986, fig. 7). The term Caridea is well known and in common usage and, therefore, I would propose to continue its use recognising within it a taxon Procarididea Chace and Manning, to include the two genera *Procaris* and *Vetericaris*, and a second taxon Eucaridea to include the remaining caridean taxa.

The taxon Stenopodidea continues to be problematic. De Saint Laurent (1979a) and others (Felgenhauer and Abele, 1983; Schram, 1984; Abele and Felgenhauer, 1986) considered the Stenopodidea to be an independent taxon more closely related to reptants than to any other group. The molecular analysis of Kim and Abele (1990) and that reported here supports these earlier results. In addition, as mentioned above, the spermatozoan morphology of *S. hispidus* (Felgenhauer and Abele, 1991; Jamieson, 1991) is unlike that of any other decapod known, emphasising its rather isolated position.

There has been considerable discussion over the classification and phylogeny of the Brachyura (see Rice, 1980, 1983). Recent data on spermatozoan ultrastructure (Jamieson, 1989, 1990, 1991) and nucleotide sequences of 18S ribosomal RNA (Spears *et al.*, in prep.) support the exclusion of the Dromiacea from the Brachyura as well as the inclusion of the Raninidae in the Brachyura. The notion of the Podotremata, Heterotremata and Thoracotremata as taxonomic or phylogenetic units based on the location of the male and female genital openings appears to be unwarranted, for these groups appear to be morphological grades, as stated by Guinot (1977), rather than phylogenetic groupings.

The challenge now facing those interested in

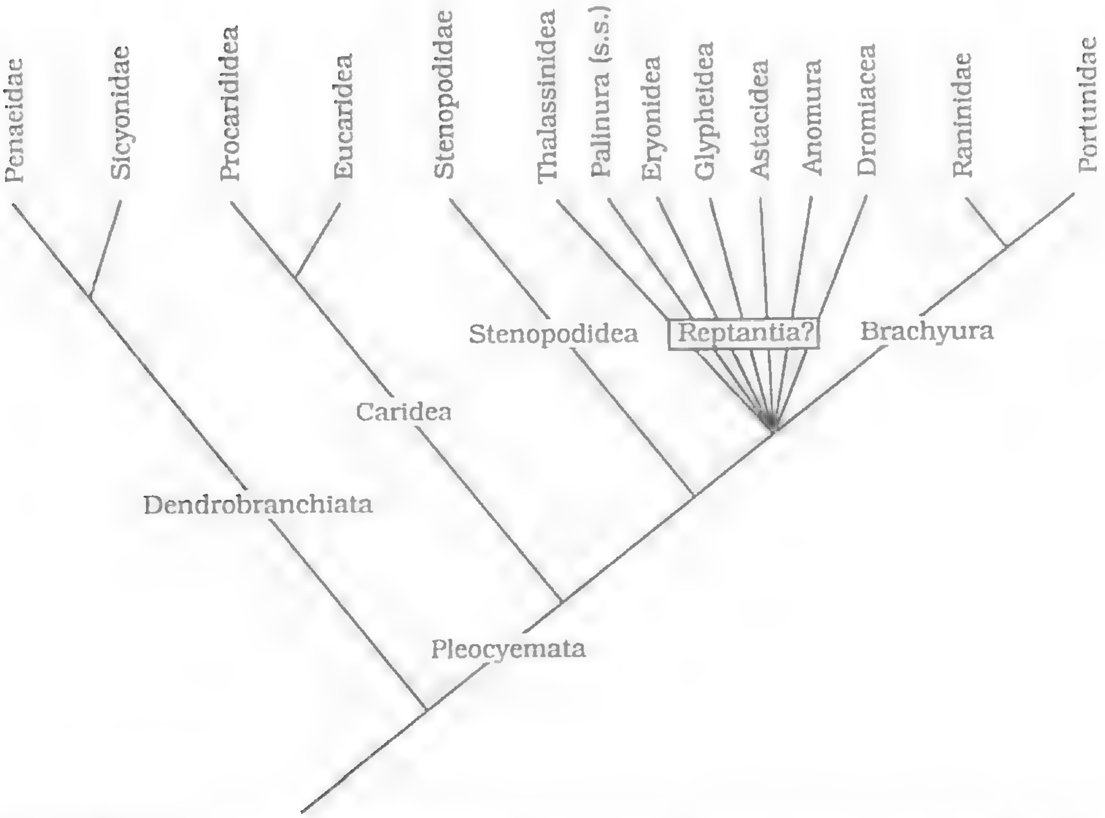

FIG. 2. Summary of phylogenetic relationships of the Decapoda based on both molecular and morphological data.

decapod evolution centres on taxa placed in the Reptantia. There seem to be as many groupings of these taxa as there are authors who have studied them. De Saint Laurent (1979a) and Burkenroad (1981) did not evaluate phylogenetic relationships but simply listed the groups that each recognized as belonging to the Reptantia if indeed such a group is even valid. For example, De Saint Laurent (1979a) listed the following reptant taxa: Scyllaridea, Eryonidea, Glypheidea, Astacidea, Thalassinacea, Anomala, Dromiacea, and Brachyura. Burkenroad (1981) listed only the Palinura, Astacina, Thalassinidea, Anomala, and Brachyura. Bowman and Abele (1982) and Schram (1986) listed the Astacidea, Thalassinidea, Palinura, Anomura, and Brachyura as infraorders in the Suborder Reptantia. The major differences among the authors are that De Saint Laurent (1979a) splits the Palinura into the Scyllaridea (although by priority of the constituent taxa one might select Palinuridea as the appropriate name), Glypheidea and Eryonidea and separates the Dromiacea from the Brachyura. The recognition of the Glypheidea as a distinct lineage by De Saint Laurent is based on study of the only extant member of this group, *Neoglyphea inopinata* (Forest and De Saint Laurent, 1981). She further suggested that the form of eryonid referred to as *Eryoineicus* is an adult secondarily adapted to a bathypelagic existence rather than a larval form as suggested by others. In addition, Burkenroad (1981) pointed out that eryonoids differ in a number of features from scyllarids and questioned the unity of the Palinura. Hence, there appear to be sufficient differences among the members of Palinura (*sensu lato*) to warrant separating the groups, especially to call attention to the need for further study. Although some preliminary molecular data are available (unpublished) they are insufficient to comment further at this time. There are also sufficient differences, noted by De Saint Laurent (1979b), among members of the Thalassinidea to raise questions about the phylogenetic status of this taxon.

In conclusion, a proposed phylogeny summarising our current knowledge based on morphological and molecular data is given in Fig. 2. The major questions that remain concerning decapod phylogeny and classification at the 'Infraorder' level are with the so-called reptant groups.

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APPENDIX I. LIST OF CHARACTERS AND CODES USED. ASTERISKS INDICATE CHARACTERS THAT MAP WITHOUT HOMOPLASY

ANTENNA II
*1. Scaphocerite present (0), reduced or absent (1)
MAXILLA 1
2. Palp; present and segmented (0), fused (1), absent (2)
THORACOPOD I (MAXILLIPED 1)
3. Modified as a maxilliped; no (0), yes (1)
4. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1), absent (2)
5. Exopod; pediform with flagellum (0), lamellar with flagellum (1), lamellar without flagellum (2)
6. Exopodal lobe (= caridean lobe); present (1), absent (0)
THORACOPOD II (MAXILLIPED II)
7. Modified as a maxilliped: no (0), yes (1)
8. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1). pediform (0), lamelliform (1)
THORACOPOD III (MAXILLIPED III)
9. Modified as a maxilliped; no (0), yes (1)
10. Endopod; 7 segments (0), <7 segments (fused and/or rudimentary) (1), completely fused (2)
PEREIOPOD I
11. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
*12. Exopod; present (0), reduced (1), absent (2)
PEREIOPOD II
13. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
*14. Exopod; present (0), absent (1)
PEREIOPOD III
15. Distal segments of endopod; achelate (0), subchelate (1), chelate (2)
*16. Exopod; present (0), absent (1)
PEREIOPOD IV
*17. Exopod; present (0), absent (1)
PEREIOPOD V
*18. Exopod; present (0), absent (1)
THELYCUM
19. Thelycum on female; present (0), absent (1)
PLEOPOD I
*20. Petasma; present (0), absent (1)
21. Appendix interna; present (0), absent (1)
22. Appendix masculina; present (0), absent (1)
*23. Configuration of pleopod; biramous (0), uniramous (1)
PLEOPOD II
24. Appendix interna; present (0), absent (1)
25. Appendix masculina; present (0), absent (1)
PLEOPOD III
26. Appendix interna; present (0), absent (1)
PLEOPOD IV
27. Appendix interna; present (0), absent (1)
PLEOPOD V
28. Appendix interna; present (0), absent (1)
UROPOD
29. Diaeresis; absent (0), present (1), present with accessory spines (2)
FOREGUT
30. Cardiac pads; absent (1), present (0)
31. Ossicles; all present (0), loss of some (1), loss of all (2), modified (3)
DEVELOPMENT
*32. Larva: nauplius (0), zoea (1)
*33. Eggs; free (not incubated) (0), attached to pleopods (incubated) (1)
GILLS
34. Gill structure; dendrobranchiate (0), trichobranchiate (1), phyllobranchiate (2)
SECOND ABDOMINAL PLEURON
35. Arrangement of second pleuron; nonoverlapping (0), overlapping (1)
BRANCHIAL FORMULA
Maxilliped III
36. Podobranch; present (0), absent (1)
37. Arthrobranch; two present (0), one present (1), absent (2)
38. Pleurobranch; present (0), absent (1)
Pereiopod I
39. Podobranch; present (0), absent (1)
*40. Arthrobranch; two present (0), one present (1), absent (2)
*41. Pleurobranch; present (0), absent (1)
Pereiopod II
42. Epipod; present (0), absent (1)
43. Podobranch; present (0), absent (1)
*44. Arthrobranch; two present (0), one present (1), absent (2)
45. Pleurobranch; present (0), absent (1)

Pereiopod III
46. Epipod; present (0), absent (1)
47. Podobranch; present (0), absent (1)
*48. Arthrobranch: two present (0), one present (1), absent (2)
49. Pleurobranch; present (0), absent (1)

Pereiopod IV
50. Epipod; present (0), absent (1)
51. Podobranch; present (0), absent (1)
*52. Arthrobranch; two present (0), one present (1), absent (2)
53. Pleurobranch; present (0), absent (1)

Pereiopod V
54. Epipod; present (0), absent (1)
55. Podobranch; present (0), absent (1)
56. Arthrobranch; two present (0), one present (1), absent (2)
57. Pleurobranch; present (0), absent (1)

APPENDIX II. INPUT DATA MATRIX

Taxon	111111111122222222223333333333444444444455555555 123456789012345678901234567890123456789012345678901234567
Euphausia	010000000000000000000000000000100000000000000000000000000
Penaeus	001020101020202000001101111111000001001000100010011001110
Procaris	011110101000000000111001111111011211111100110011001101111
Caridea	011111111120200000110000000010111211001101110111011101110
Stenopus	011000101021212111111011111100011101001000100010001001110
Axiid	121120101021210111110010000010011210010010000000001001111
Astacoid	111000101021212111011011110010011110210010001000100011110